

Taxonomy of the South Pacific brisingidan *Brisingaster robillardi* (Asteroidea) with new ontogenetic and phylogenetic information

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ABSTRACT

New material of *Brisingaster robillardi* de Loriol 1883, including juveniles, allows a more complete description of the species. Papulae, obscured in the holotype and previously unknown for this taxon, are present. Abactinal plate arrangements provide new autapomorphies for the genus *Brisingaster*. Scanning electronic microscope photographs of pedicellariae are described and compared with those of *Novodinia antillensis*. The range of *B. robillardi* is extended to New Caledonia, Western Australia and Amami-o-shima, Japan. Morphological variation is present between material from the Pacific and the Indian Ocean. *Novodinia helenae* Rowe, 1989 is synonymized with *B. robillardi*. New phylogenetic evidence also supports a new family, the Brisingasteridae, which tentatively includes *Brisingaster* and *Novodinia*.

KEY WORDS

Brisingida,
Brisingasteridae,
Brisingaster,
Novodinia,
pedicellariae,
ontogeny,
phylogeny,
taxonomy,
New Caledonia.

RÉSUMÉ

Taxonomie du brisingidé du Pacifique Sud *Brisingaster robillardi* (Asteroidea), accompagnée de données nouvelles tant ontogéniques que phylogéniques.

Brisingaster robillardi de Loriol 1883 est décrit à partir de matériel nouveau incluant des juvéniles. Les papules, masquées sur l'holotype et inconnues pour ce taxon, sont ici signalées. Une description plus pointue de l'arrangement des plaques abactinales révèle de nouvelles autapomorphies du genre *Brisingaster*. Des photographies de pédicellaires en microscopie électronique à balayage sont décrites et comparées à celles de *Novodinia antillensis*. La distribution géographique de *B. robillardi* est étendue à la Nouvelle-Calédonie, la côte ouest de l'Australie et Amami-o-shima au Japon. Des variations morphologiques existent entre les spécimens de l'océan Pacifique et de l'océan Indien. *Novodinia belenae* Rowe, 1989 et *B. robillardi* sont mis en synonymie. De nouvelles données phylogénétiques permettent d'éraier l'existence d'une nouvelle famille, les *Brisingasteridae*, qui pourrait rassembler les genres *Brisingaster* et *Novodinia*.

MOTS CLÉS

Brisingida,
Brisingasteridae,
Brisingaster,
Novodinia,
pédicellaires,
ontogénie,
phylogénie,
taxonomie,
Nouvelle-Calédonie.

INTRODUCTION

Brisingidans are a clade of suspension-feeding Asteroidea, noteworthy for holding their arms into the water column, using their pedicellariae-laden spines to capture small zooplankton prey (Emson & Young 1994). They are found at a depth range of 200-6900 m. Brisingidans are most diverse in the Indo-Pacific region but they occur in all of the world's oceans.

The taxonomy of Atlantic brisingidans was reviewed by Downey (1986) and Clark & Downey (1992). No equivalent on Pacific brisingidans is available. Studies of Pacific brisingidans (e.g., Fisher 1917, 1919, 1928) are in need of re-evaluation. The present paper treats one poorly known taxon. Although reviewed by Fisher (1917, 1919, 1928, 1940), *Brisingaster robillardi* de Loriol, 1883, was previously known only from the holotype. While gathering data for a phylogenetic analysis of the Brisingida (Mah 1998a, 1998b) additional specimens of *B. robillardi* were identified among material borrowed from the Muséum national d'Histoire naturelle. These specimens and others extend the geographic range and add phylogenetic and morphological information to our knowledge of this species.

MATERIALS AND METHODS

Fourteen dry and two wet specimens were examined. Measurements include disc diameter (Dd), the distance between the center of the disc to the arm tip (R) and the radius of the disc measured from the center of the disc to its edge (r). Other terminology follows usage established by Blake (1989), and Spencer & Wright (1969).

Repositories include:

- | | |
|-------|--|
| CASIZ | Department of Invertebrate Zoology,
California Academy of Sciences; |
| LACM | Los Angeles County Museum of
Natural History; |
| MHNG | Muséum d'Histoire naturelle (Genève) |
| MNHN | Muséum national d'Histoire naturelle
(Paris); |
| AM | Australian Museum; |
| WAM | Western Australian Museum. |

SYSTEMATICS

Order BRISINGIDA

Family BRISINGASTERIDAE Mah, 1998

Genus *Brisingaster* Loriol, 1883

Brisingaster robillardi Loriol, 1883

Brisingaster robillardi Loriol 1883: 55. — Fisher 1917: 419; 1919: 502; 1928: 5; 1940: 205. — Spencer & Wright 1966: U78. — Clark & Downey 1992: 464.

MATERIAL EXAMINED. — **Mauritius.** Île Maurice, 60 brasses (holotype of *B. robillardi* MHNG 79419). **Western Australia.** Off Norfolk Island, 309 m (holotype of *Novodinia helena* AM J21703). — R/V *Lady Basten*, stn LB7, S. of Bedwell I., Clerke Reef, 17°54.2'S, 119°17.5'E to 17°53.3'S, 119°17.1'E, 200 m, rocks and hard sponges, 18.VIII.1995, coll. L. M. Marsh *et al.* (WAM Z2737). — Off Norfolk Island Ridge, Seamount Trygon, 24°40.12'S, 168°9.97'E, 820-1220 m, 20.XI.1996, coll. T. Iwamoto (1 specimen wet CASIZ 108495).

New Caledonia. Programme Lagoon, N/O *VAUBAN*, stn 421, Nouméa, 22°45.6'S, 167°06'E, 315 m, 24.I.1985, coll. by B. Richer de Forges ORSTOM (2 specimens dry MNHN).

BERYX 11, N/O *Alis*, stn DW11, Sud Nouvelle-Calédonie, 24°44'S, 168°10'E, 320-350 m, 16.X.1992, coll. by B. Richer de Forges, ORSTOM (2 specimens dry MNHN). — Stn CH15, 24°44'S, 168°08'E, 225-250 m (1 specimen dry MNHN).

BATHUS 2, N/O *Alis*, stn DW717, Sud Nouvelle-Calédonie, 22°44'S, 167°16.6'E, 350-383 m, 11.V.1993, coll. by P. Boucher & Richer de Forges ORSTOM (3 specimens dry MNHN).

BATHUS 3, N/O *Alis*, stn CH801, off Norfolk Ridge, 23°39'S, 168°00'E, 270-300 m, 27.XI.1993, coll. by P. Boucher, Richer de Forges, ORSTOM & Warren (1 specimen dry MNHN). — Stn CP806, Norfolk Ridge, 23°42'S, 168°01'E, 308-312 m (1 specimen dry MNHN).

CHACAL 2, N/O *Coriolis*, stn CP26, off Norfolk Ridge, 23°18'S, 168°04'E, 296 m, 31.X.1986 (1 specimen dry MNHN).

Japan. R/V *Toyoshio-Maru*, SE off Amami-o-shima, Amami-shoto, 28°04.70'N, 129°27.40'E, 302 m, 11.XI.1995, coll. Mark Grygier *et al.* (LACM 95-87.1).

TABLE 1. — Synapomorphies of the *Brisingasteridae* numbers refer to characters labelled on Fig. 5.

1. Squarish (L:W = 1:1) ambulacral ossicles
2. Squarish (L:W = 1:1) adambulacral ossicles
3. Large fan-shaped mouth angle plates blocking junction between mouth and tube fort groove
4. Truncate adambulacral spines

SYNONYMY OF *NOVODINIA HELENAE* ROWE 1989

Examination of the holotype of *Novodinia helena* Rowe, 1989 reveals it to be a synonym of *Brisingaster robillardi* de Loriol, 1883. As discussed below, *Novodinia* and *Brisingaster* are sister taxa, united by several synapomorphies (Table 1). An open reticulate abactinal skeleton, an oral frame articulated with an externally expressed crown of abactinal disc plates and other characters outlined in Table 2 are present in the holotype of *N. helena* clearly distinguishing it as *Brisingaster*. The holotype of *N. helena* also lacks a fenestrate skeleton, an autapomorphy of *Novodinia*.

One character differs between the holotype of *B. robillardi* and the holotype of *N. helena* (see below). Additional specimens from the type locality may reveal additional apomorphies differentiating the Indian from the Pacific forms of *Brisingaster*.

If this were to be the case, the Indian form,

TABLE 2. — Compared characters of *Brisingaster* versus *Novodinia*. Numbers refer to autapomorphies labelled on Fig. 5

<i>Brisingaster</i>	<i>Novodinia</i>
5. Abactinal skeleton arranged into an open mesh plate.	Abactinal disc with an abutting pavement of discoid plates.
6. Reticulate, open mesh-like, abactinal skeleton.	11. Fenestrate abactinal skeleton.
7. Oral frame articulated with externally expressed crown of abactinal disc plates.	Oral frame entirely internal.
8. Central cluster of abactinal disc plates.	No central cluster of abactinal disc plates.
9. Inverted Y-shaped plate at the base of arm.	Inverted Y-shaped plate absent.
10. Small cluster of four abactinal plates at the apex of each interradius.	Small cluster absent.

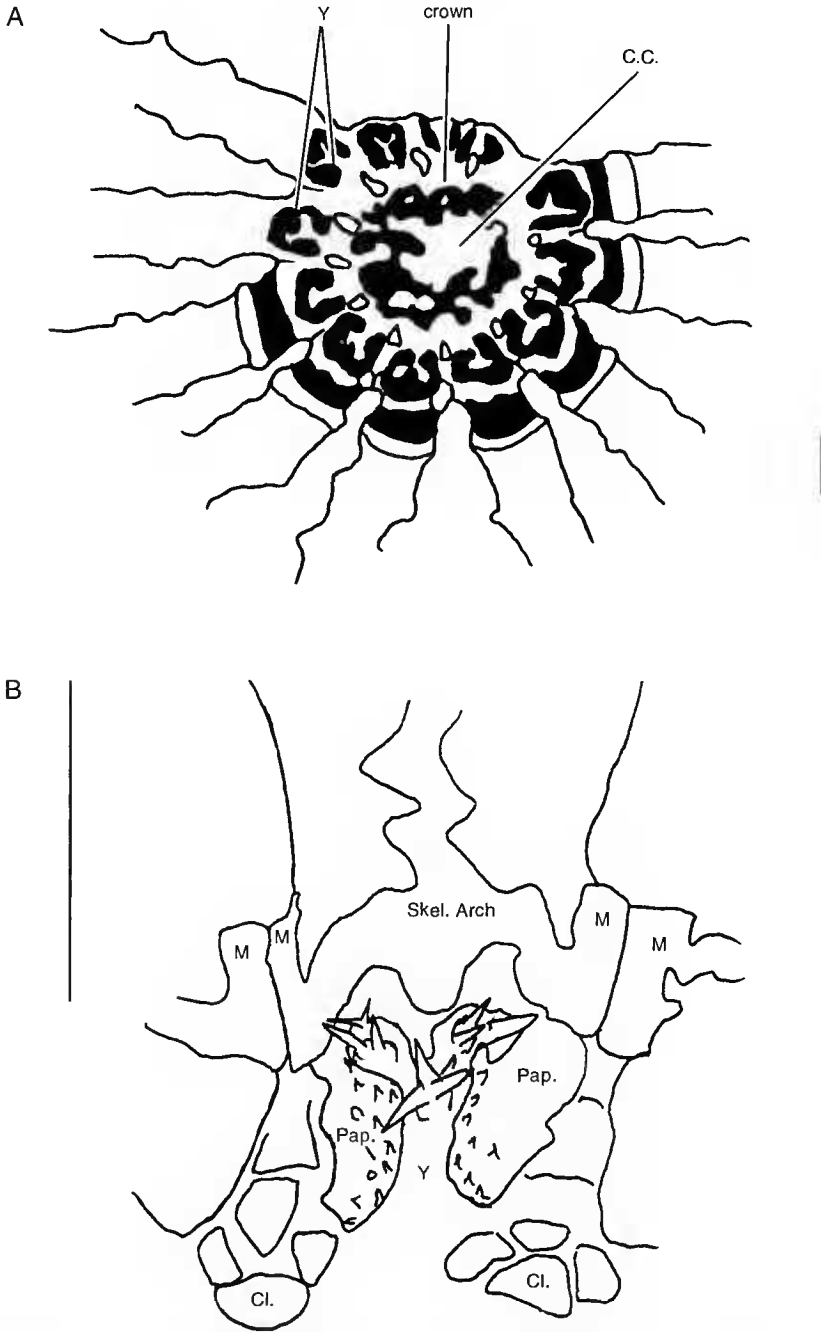


FIG. 1. — **A**, abactinal side of specimen from MNHN Programme Lagoon, stn 421 showing crown of abactinal plates. Crown is connected to oral ring via plates in each interradii, darkened regions represent integument between skeletal arches and papular regions, Y-upside-down Y-shaped plate, C.C. central cluster of abactinal plates; **B**, abactinal plates, resembling upside-down Y from abactinal surface of specimen from MNHN BERYX 11, stn DW11 with five clusters of spines, Cl. represents flat cluster of plates at the apex of each interradii, M-Marginal plates, Pap.-Papular regions, Skel. Arch-first skeletal arch, Y-upside-down Y-shaped plate. Scale bars: A, 1.0 cm; B, 0.5 cm.

represented by the holotype of *B. robillardi*, would be a separate species from the Pacific form, represented by the holotype of *N. helenae*. This would result in the reassignment of *Novodinia helenae* Rowe 1989, as *Brisingaster helenae* (Rowe 1989). However, the material reported herein supports recognition of only one wide ranging species. Thus, *Novodinia helenae* Rowe 1989, is a synonym of *Brisingaster robillardi* de Loriol, 1883, and should enter in synonymy.

REVISED DIAGNOSIS

Characters unique to *B. robillardi* include: abactinal plates forming a reticulate open mesh on the disc, an upside-down Y-shaped plate at the base of each arm, a crown of externally expressed abactinal plates connected to the internal oral ring at each interradial, a developed cluster of abactinal plates at the center of the disc and a small cluster of four spineless abactinal plates at the apex of each interradial. These characters are all outlined in Table 2.

Plesiomorphic (phylogenetically uninformative) but useful diagnostic characters include: papulae on the disc and arms, spade-shaped MAPs that abut into the tube foot groove, squarish ($L = W$) ambulacrals and adamambulacrals and truncate adambulacral spines. These characters are outlined in Table 1. Eleven to thirteen arms are present.

DESCRIPTION

The disc is abactinally flattened in some specimens (e.g., MNHN Programme Lagoon, stn 421) but concave in others (e.g., MNHN BATHUS 2, stn DW717). Specimen character measurements such as R , r , Dd , etc. are summarized in Table 3.

The abactinal disc plates form a confluent reticulated network with the skeletal arches (= costae) on the arms (Fig. 1A, C). These plates are diamond to rhomboid and overlap one another forming the network on the disc. Abactinal plates form variably sized meshes on the disc but are arranged into distinct patterns (Fig. 1A, B). Thickness of abactinal plate varies with the size of the specimen. Disc plates on the abactinal disc plates of the largest three specimens (MNHN

BATHUS 2 stn DW717 (#1), $dd = 1.9$; WAM Z2737, $dd = 2.4$ cm; MNHN BERYX 11 stn DW11, $Dd = 2.5$ cm) are much more elaborate and thicker than those in other specimens. At the center of the abactinal disc surface is a heavily calcified cluster of plates. Presumably the anus is located within this calcified center, although this was not observed in any of the specimens.

Individuals with smaller disc diameter (e.g., MNHN Programme Lagoon, stn 421) have thinner skeletal arches (0.5 mm thick) than individuals with larger disc diameters (e.g., MNHN BERYX 11, stn DW11) and thicker skeletal arches (1.0 mm thick). The number of costae on smaller specimens ($dd \leq 1.2$ cm) also seems to be less than those in larger specimens ($dd \geq 1.9$ cm). Large thorny spines are found on these plates, usually one large spine and two to three accessory ones. Disc spines "united by a web across which the pedicellariae span" as described by Rowe (1989: 275) are probably damaged pedicellarial sheaths that have been torn off spines during collection by dredge or trawl nets.

Four to fifty papulae are present between the open meshes of the abactinal disc surface. Hundreds of papulae are present in the intercostal regions between skeletal arches on the arms.

Four to eight costations are present on each arm. Fewer costae are found on smaller specimens. Eight thick skeletal arches are found on the specimen with the largest disc diameter (MNHN BERYX11, stn DW11, 2.5 cm). Costae are present on the gonadal, or proximal, section of the arms. Full abactinal costae end abruptly and continue onto the distalmost half of the arms as paired remnants on either side of the arm. Skeletal arches are thicker proximally than distally. The costae from the lateral sides of the arm meet on the abactinal surface, forming an irregular array of arches, zig-zags and loops. Paired arches of remnant costae each possess three to five prominent lateral spines often covered with pedicellariae. Skin on the distal half of the arm is translucent.

Ambulacral ossicles are clearly visible through the integument along the distal half of the arm. Ambulacrals are block-shaped (with $L:W$ ratio of 1:1) proximally, then becoming more slender ($L:W$ ratio of 1:0.4) distally, attenuating towards the tip.

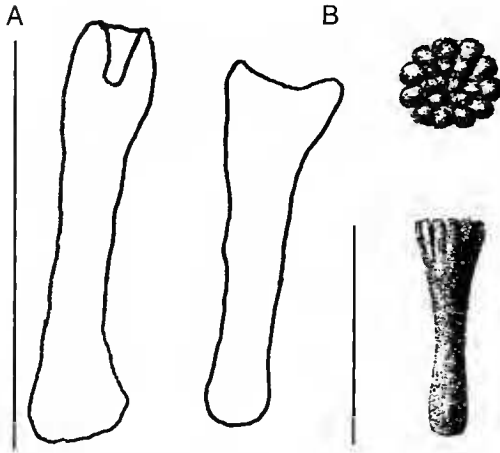


FIG. 2. — A, Adambulacral spine from *B. robillardii* off New Caledonia (MNHN BERYX 11, stn DW11); B, adambulacral spine from de Lorient (1883: pl. 6, #1) holotype *B. robillardii* off Mauritius (MHNG 79419). Scale bars: A, 4.0 mm; B, 2.5 mm.

The terminal plate is unknown.

The disc ossicles form a complex consisting of an internal fused oral ring connected to externally visible abactinal plates (Fig. 1A). Abactinal plates form a distinct crown on the disc separate from, but connected to, the oral ring. This crown is attached to the oral ring via three ossicles, two single and one paired, in each interradial arc. A junction of four abactinal plates forms a thick flat spineless cluster at the apex of each set of connective ossicles in each interradial arc on the abactinal side of the disc. This last paired element articulates with the marginal plate abutting against the proximal adambulacral ossicles forming part of the nonmuscular syzygy in each interradius. Frequently this marginal plate is connected to the first skeletal arch. The plate either joins the skeletal arch completely or bypasses it forming a perpendicular upside-down T with it. This network of abactinal disc plates forms a distinct articulation with the costae. The abactinal disc plates connect to the nonmuscular syzygies in each interradial arc. Pairs of the abactinal plates conjoin to form the first skeletal arch on each arm.

Abactinal plates, resembling an upside-down Y, sit at the base of each arm near the junction with the disc (Fig. 1B). This plate sits in the center of

a roughly quadrature enclosure of papulae sitting at the abactinal junction between the base of the arm and the edge of the disc (Fig. 1A, B). The upside-down Y is covered with four to eight clusters of spines each bearing two to six spinelets. At the apex of the upside-down Y on the abactinal radii of the disc lies a single prominent spine cluster with four to six spinelets. Three spine clusters with two to three spinelets each sit on each arm of the upside-down Y. One cluster with one to two spinelets is present subapically above the arms of the Y. The number and arrangement of plates, and spine clusters for each radii is inconsistent and can vary within a single individual. These plates also occasionally abut against the first skeletal arch.

The arrangement of the plates forming the upside-down Y varies. They can form a very distinct Y or an archipelago of island-like ossicles in an approximate Y-shaped formation (Fig. 1B). On the disc, the arms of the upside-down Y separates a pair of relatively large papular regions. This paired arrangement of papular areas is present on all specimens examined and appears to be an autapomorphy for *B. robillardii*.

In addition to the nonmuscular syzygy of the first pair of adambulacrals, a marginal plate lies over the second and third adambulacrals fusing them together. This plate extends above the paired third and sometimes fourth pair of adambulacrals but does not fuse them together. In smaller individuals (e.g., MNHN BATHUS 2, stn 717, #2, #3) the first pair of adambulacrals are directly fused but the marginal plate has not yet fully fused together with the second and third adambulacral pairs. These latter two adambulacral pairs are completely separate, not fused.

One to three triangular, denticle-shaped, spineless, marginal plates occur between the skeletal arches. The angles of these plates abut the junctions between the adambulacral plates. Marginal plates are adjacent but alternate with the adambulacrals. As in all brisingidans, actinal plates are absent.

A single adambulacral spine is present for every adambulacral plate. The first and second adambulacrals end in a pointed tip. Subsequent adambulacral spines are truncate. In the specimens from the South and Central Pacific, tips of the

A



B



C

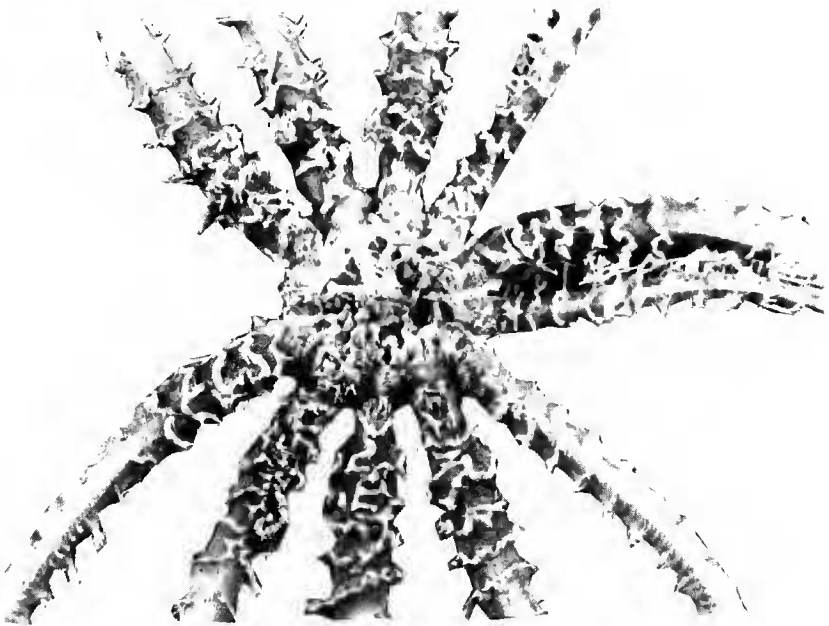


FIG. 3. — A, scanning electron microscope photo of lateral spine pedicellariae from holotype of *Novodinia helenae* (AMJ21703); B, scanning electron microscope photo of lateral spine pedicellariae from *Brisingaster robillardii* (MNHN, BATHUS 2, stn DW717, #1). Scale bar: A, 30 μ m; B, 35 μ m.

truncate adambulacral spines are composed of two prongs with a bony web filling in the space between them (Fig. 2A). In the holotype (Indian Ocean), approximately 20 blunt spinelets adorn the proximal adambulacral spine tips (Fig. 2B).

Adambulacral spines in smaller individuals seem to be proportionally smaller. Spine tips in smaller individuals (e.g., one specimen from MNHN DW 717 w/ dd = 0.8 cm) resemble those in adults but are smaller. In some specimens (e.g., LACM 95-87.1) the spine tips have been worn off and appear more acicular.

Elongate lateral spines first occur at approximately the seventh to ninth adambulacral plates at the base of the second to third skeletal arch. Lateral spines are typically absent (except for one side of one arm in specimen from MNHN BERYX 11, stn CH15) from the base of first costae. Distally on the arm, four to five thorn-like spines lie on the lateral sides of the arm on the costae. Each ossicle composing the skeletal arch is armed with approximately one spine.

Pedicellariae occur on spines in densities of approximately 20/mm². Pedicellariae were sampled from the holotype of *Novodinia helena* and from a specimen of *B. robillardi* (MNHN BATHUS 2, stn DW717) for SEM photos. Owing to the condition of the holotype (see below), pedicellariae could not be successfully extracted from the holotype of *B. robillardi* for SEM.

Valves from the individuals sampled are identical in overall morphology (Fig. 3A, B). They measure approximately 105-112 μ m in length, 35 μ m in width at the base, 21 μ m in width at the centrally recurved areas and approximately 28 μ m in width at the tip of the jaw. Teeth occur in two areas, the valve tip (or jaw) and an inner medial projection. On the jaw, three rows of teeth-like spines occur between the two large canine-like projections (\approx 10 μ m in length). The third innermost row of four spines possess the largest of the teeth (\approx 6 μ m in length) preceded by a row of five spines (\approx 3 μ m). The shortest teeth (\approx 2 μ m) occur in the first row. Eight teeth lie in this row. These three rows appear to be staggered with respect to one another. These teeth interlock with teeth on the complimentary valve. A row of four to five spines in decreasing size occur

laterally on the jaw of the pedicellarial valves. The medial projection bears two to three poorly defined rows of short spinelets (2-3 μ m). The bases of the valves are broadly spatulate and perforated, with an inner surface excavated to accommodate muscle attachment as observed by Emson and Young (1994).

Pedicellariae of *B. robillardi* have been figured before only twice, by de Loriol (1883: pl. 6, fig. 1) and Rowe (1989: fig. 11C). Aside from the detailed work of Emson & Young (1994) no SEM photos of brisingidan pedicellariae currently exist in the literature. Aside from the slightly larger sized valves of *N. antillensis* (150 μ m) versus those of *B. robillardi* (112 μ m) the pedicellariae morphology of the two species are practically indistinguishable. Given the close phylogenetic relationship between *Novodinia* and *Brisingaster* (as described below) pedicellariae morphology may provide another potential source of synapomorphies for the two taxa.

Mouth angle plates (MAPs) are fan-shaped. A gap filled with connective tissue is present between the paired MAPs at each interradial. A large round flange from each paired MAP juts into the tube foot groove. Three to five spines project from each of the MAPs. Of these spines, two to three of them interdigitate, clasping with the MAP spines on the opposite side of the furrow separating the tube foot groove from the mouth. The innermost spines, found nearest the tube foot groove, are usually very small as opposed to the largest spines found on the outermost side of the MAP projecting into the mouth. These larger mouth spines typically have sheaths of pedicellariae.

Smaller specimens (dd = 0.6 cm to 1.6 cm) typically have between three and four spines whereas larger specimens (1.7 to 2.5 cm) typically have five. An additional spine is sometimes present on the actinal surface of the MAP adjacent to the first adambulacral plate.

Actinal MAP spines are absent on the holotype of *Novodinia helena*. Specimen MNHN BATHUS 2, stn DW 717 possesses one small arm undergoing what appears to be regeneration. This arm has small thorny adambulacral spines, only two skeletal arches, and tiny lateral spines at the base of the first skeletal arch. As with the

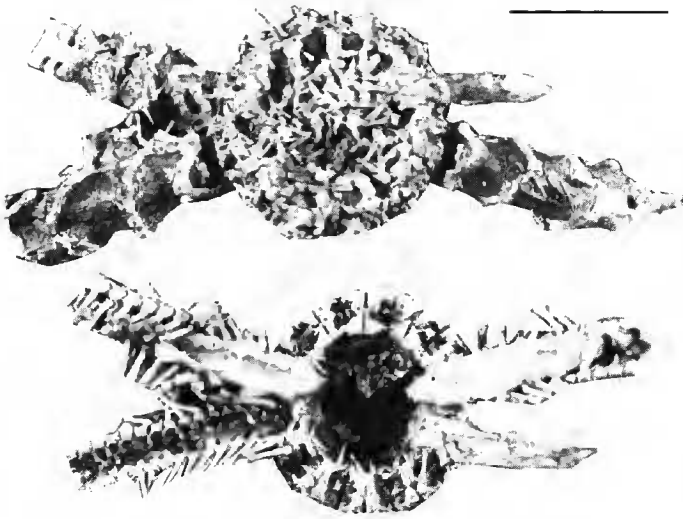


FIG. 4. — **A**, holotype of *Brisingaster robillardii* (MNHNG 79419); **B**, abactinal side of the same specimen showing stream of resin across disc and arms. Scale bar: 1.0 cm.

other spines, pedicellariae are present on the spines. Small marginals are present on this arm.

Madreporite diameter varies in size from approximately 0.12 cm in specimen with Dd = 1.4 cm and 1.6 cm (AM J21703 and MNHN BATHUS 3, stn CH 801 respectively) to 0.2 cm in specimen with Dd = 1.9 cm (MNHN BATHUS 2, stn DW 717). Madreporite diameter appears to be larger in specimens with greater Dd. Madreporite is coarsely furrowed and is distinctly raised above the disc surface (e.g., height of madreporite in MNHN BATHUS 2, stn DW717 = 1.0 mm).

Gonads are serial. Five gonad sacs, occur on either side of the ambulacral ossicles. In CASIZ 108495 each of these sacs are 0.4 cm in length.

Color of pre-preserved CASIZ 108495 was an overall red-orange with a bright orange ring around the edge of the disc and on the arms. Color in alcohol is white. Dry specimens have light cream to dark brown colored abactinal skeleton and ambulacral ossicles with dark tan intercostal and papular areas.

REMARKS ON THE HOLOTYPE

On the holotype of *B. robillardii* (MNHG 79419, Fig. 4A) practically all of the abactinal disc spines have been lost, leaving only spine bosses. Several abactinal plates along the radii of

the disc at the bases of the arms are present but finer spination is absent.

The holotype is covered with a resin that has accumulated small bits of debris obscuring finer details on the test (such as spine bosses). Intercostal areas on the arms and papular areas on the disc are also badly obscured by very fine dirt.

Abundant papulae are present in the skin between the arm costations and abactinal disc plates. This important characteristic is obscured on the holotype and is absent from Perrier's original description and from later accounts (e.g., Clark & Downey 1992: 463, table 75). Clark & Downey (1992: 463, table 75) have also described the presence of "fenestrate plates" between the costations. Based upon examination of the type, it seems that dried papulae and/or debris may have been misinterpreted as fenestrate plates. No plates occur between the costations on the arms of *B. robillardii*.

A thick stream of resin is present across the threshold between the mouth and the tube foot groove obscuring details of the MAPs, including spination (Fig. 4B).

ECOLOGY AND BIOGEOGRAPHY

Photographs of the topology and ecology of the New Caledonian locality (approximately 23°S, 166°E) were described by Roux (1994), who

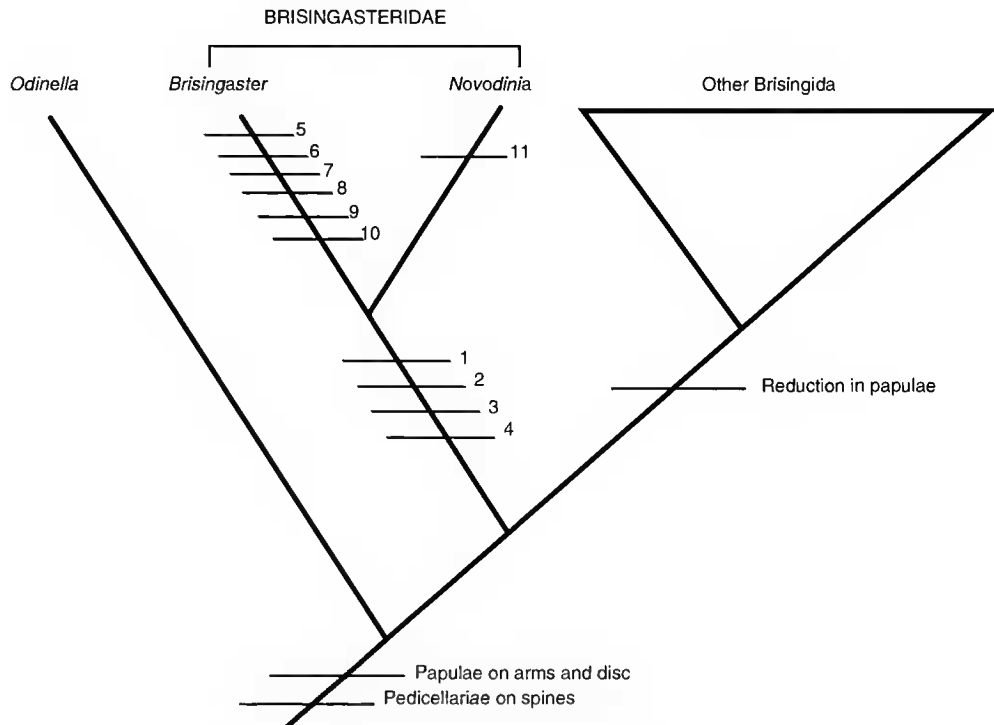


FIG. 5. — Abbreviated phylogenetic tree of the Brisingida showing basal brisingidans, *Odinella*, *Brisingaster*, *Novodinia*. Numbers correspond to autapomorphies outlined in Tables 1 and 2.

noted a subvertical wall of a fault escarpment inhabited by very dense population of suspension feeding echinoderms, including ophiacanthid ophiuroids, bourgueticrinid stalked crinoids and unidentified brisingidan asteroids (Roux 1994: 19). Brisingidans are present in greatest numbers on the escarpment overhang and on ridges of the subvertical wall (Roux 1994: figs 11; 22). Brisingidans shown in Roux (1994: figs 11; 22) are consistent with *Brisingaster robillardi*. Although a positive identification is not possible from photos. Unpublished images provided by M. Roux also show brisingidans with fifteen arms that could either be *Brisingaster* or *Novodinia*.

The type locality of *B. robillardi* is Mauritius ("île Maurice") from 109 m ("60 brasses"). MNHN material collected from south of New Caledonia, and the Isle of Pines, southeast of

New Caledonia, at 225-1200 m, extend the range of this species to the South Pacific. A single specimen, LACM 95-87.1, from a depth of 302 m, extends the northern range of *B. robillardi* to the Amami-o-shima islands in the Central Pacific. Two specimens, WAM Z2737 and CASIZ 108495, extend the range of this species off the coast of Western Australia at a depth range of 200-1220 m. The localities suggest a widespread distribution of this species throughout the South and Central Pacific. Aside from the holotype, no other specimens are known from the Indian Ocean.

PHYLOGENETICS OF *BRISINGASTER*

Fisher (1917: 419, 1919: 502) was the first to suggest a relationship between *Brisingaster* and

TABLE 3. — Specimen Measurements. Measurements are in centimeters. Dd= Disc; diameter, R= Distance; between center of disc to arm tip, r= Distance from disc center to edge, arms= Number of arms, C= Number of costae, MS= Number of MAP spines.

Specimen	Dd	R	r	W	arms	C	MS	Additional Remarks
MHNG 79419 (holotype <i>B. robillardii</i>)	1.5	7.5	.8	.51	12	4 to 5	5	specimen damaged, see text
AM J21703 (holotype <i>N. helenae</i>)	1.4	7.5	.7	.38	12	4 to 5	3 to 5	
MNHN Programme Lagoon stn 421 (#1)	1	4	.5	.2	12	5	3 to 4	
stn 421 (#2)	1	4	.5	.2	12	5	3	
BERYX 11, stn CH15	1.5	9.5	.8	.8	12	6 to 7	5	
BATHUS 3, stn CH801	1.6	7	.8	.45	13	5	3	small crustacean husk and sponge in mouth
CHALCAL 2, stn CP26	1.7	6	.9	.5	12	6 to 7	3 to 5	four crustacean husks in mouth
BATHUS 3, stn CP806	1.8	6.5	.9	.55	12	7	4 to 5	w/ two regenerating arms
BERYX 11 stn DW11 (#1)	2.5	6.5	1.3	.7	13	7 to 8	5	
stn DW 11 (#2)	1.8	8	.9	.7	12	5 to 6	4 to 5	small amphipod on adambulacral spine
BATHUS 2 stn DS717 (#1)	1.9	8	.9	1	12	7 to 8	5	w/ one arm regenerating
stn DS 717 (#2)	.8	3.3	.4	.13	12	4 to 5	4	
stn DS 717 (#3)	.65	2.5	.4	.15	12	3 to 4	2 to 3	w/ sponge chunk in mouth w/ small ophiuroid on abactinal surface
CASIZ 108495	1.8	5.5	.9	.8	12	4 to 7	5	
LACM 95-87.1	.9	3.2	.45	.25	11	3	5	
WAM Z2737	2.4	8.5	1.2	1	13	11	5	

Novodinia (formerly *Odinia*) and later to *Odinella* (Fisher 1940: 205). Preliminary phylogenetic results by Mah (1998a, 1998b) showed *Odinella* as the sister taxon to the crown brisingidan clade with *Novodinia* and *Brisingaster* as sister taxa within that clade (Fig. 5). *Odinella*, *Novodinia*, and *Brisingaster* are basal on the tree relative to other brisingidan taxa (Fig. 5). These taxa possess plesiomorphic brisingidan characters, including papulae on arms and disc, a distinct gap between the MAPs, and a non-muscular fusion of basal adambulacrals. The clade supporting *Novodinia* and *Brisingaster* is supported by synapomorphies shown in Table 1. Autapomorphies of *Brisingaster* are outlined in Table 2. *Brisingaster* and *Novodinia* are tentatively designated as a new family, the Brisingasteridae (Mah 1998a). *Odinella* is assigned to a new monotypic family, the Odinellidae.

Depth distributions mapped onto a phylogeny of the Brisingida (Mah 1998a, 1998b) show that basal brisingidans inhabit a much shallower depth-range (100-1400 m) relative to more

recently evolved brisingidans (e.g., the Freyellidae).

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